AGE GROUPS AND LONGEVITY IN THE AMERICAN ROBIN [1]

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THE published accounts of age studies and observations on birds are generally classifiable into three groups. The first group contains those observations, derived largely from records kept by zoos, of ages of birds kept in captivity. Among the more important compilations of this type are those of Gurney (1899), Mitchell (1911), Flower (1926, 1931), Brown (1928), and Groebbels (1932). Such data are valuable in that they give indications of the *potential longevity* of the species.

The second group is that which deals with *potential natural longevity*. This type of information is scattered in innumerable papers and notes and in bird-banding reports. Some of the more comprehensive sources of such data are the compilations of Mortenson (1926), Nichols (1927), Lafranchise (1928), Groebbels (1932), and the numerous reports of Thomson in *British Birds,* Schenk in *Aquila,* Thienemann in *Vogelzug* and *Journal für Ornithologie,* Drost in the same journals, Cooke and Lincoln in *Bird-Banding,* and Jägersköld in *Götesborgs Musei Arstryck.*

The third type of study deals with the *average natural longevity,* survival and mortality rates, and the age-group composition of populations. Because studies of this type must be based on large numbers of recoveries of birds of known age (i.e., banded as young), they have been necessarily limited in number. The most thorough analyses of bird ages from a population standpoint are the excellent study of Kraak, Rinkel, and Hoogerheide (1940) on the Lapwing (*Vanellus vanellus*) in Holland, and the studies of Lack (1943 *a, b, c, d*), which give statistics on several species of British birds including the Blackbird (*Turdus merula merula*) and the Song Thrush (*Turdus ericetorum ericetorum*). In this country, Hoffman (1929) has calculated the longevity of the Blue Jay (*Cyanocitta cristata*); Magee (1928, 1936) and Whittle (1929) have made longevity estimates for the Purple Finch (*Carpodacus purpureus*); Harold and J. R. Michener (1933) have recorded age data on the House Finch (*Carpodacus mexicanus frontalis*); and Nice (1937) has studied the longevity and age-group composition of a local population of Song Sparrows (*Melospiza melodia euphonia*). Leopold *et al.* (1943) have given data on the annual mortality rate in Ring-necked Pheasants (*Phasianus colchicus*) in the University of Wisconsin Arboretum; Sumner (1935), Emlen (1940), and Richardson (1941) have published the results of similar investigations on the Cali-

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fornia Quail (*Lophortyx californica*). The data of Austin (1942) on the Common Tern (*Sterna hirundo*), unfortunately, do not give information on the average longevity of this species because many of these birds do not return to the breeding grounds where they were banded until the second season following hatching. Thomas (1934) made observations on the life span of the Starling (*Sturnus vulgaris*) but did not compute an average longevity or survival rate.

Methods and Materials

The American Robin (*Turdus migratorius*) was selected for the present study because of the relatively large number of available banding records and because of the certainty with which the young can be distinguished from adults. Since only records of birds banded as young north of the Ohio and Missouri rivers and north of the southern boundaries of Pennsylvania and New Jersey were used in this study, it is assumed that all the records apply to the northern race, *Turdus migratorius migratorius,* although it is possible that a few records of the southern race, *achrusterus,* may be included. All records of birds banded within the range of the western races *caurinus* and *propinquus,* were discarded.

The prime assumption in this study, as in those of Lack and of Kraak *et al.*, is that *a group of birds of a species which were banded as young and subsequently recovered constitutes a normal sample of the entire population of the species.* An objection may be raised to the validity of such an assumption on the grounds that (since the number of birds banded varies considerably from year to year) the conditions of the years in which large numbers of birds have been banded will be reflected disproportionately in such samples. The situation is further complicated by the possible variations in activities, such as shooting and trapping, which lead to "recoveries" and "returns" [2] of banded birds. The possibility of variations from true means because of these factors cannot be denied, but in this study no noticeable variation attributable to them has been detected.

A further objection can be raised on the grounds that some of the "causes of death" may have differential rates according to age and that the number of returns and recoveries of birds whose death is attributable to a given cause may not be proportional to the total number of deaths in the whole population due to that cause. Lack (1943*c*) has shown that in some non-passerine species shooting is differential according to age, that is, the chance of a first-year bird being shot is greater than that of an older bird. In the present study of American Robins, it is certainly unlikely that, in the case of each

[2] These terms, although not adapted to this type of study, are here used in the same sense as in migration studies, where "Returns" are banded birds taken dead or alive at the station where banded, and "Recoveries" are banded birds taken dead or alive elsewhere. The verbal form "recovered," however, is used in this paper to indicate the obtaining of banded birds *anywhere,* dead or alive; it is not used in a specialized sense.

cause of death, the number recovered is proportional to the number actually dying from this cause. However, data presented subsequently (Table 9) will show that there are probably no important differences in death rates according to various causes of death once the young birds have begun their first migration.

The records which were analyzed in this study are from the bird-banding files of the Division of Wildlife Research, United States Fish and Wildlife Service. All reports on Robins (a total of 855) which had been banded as young in the range of *Turdus m. migratorius* and subsequently recovered (either alive or dead), and for which there were adequate data were used. They extend through the period 1920–1940.

All estimates of age and longevity in this paper are calculated from the first November 1 of the bird's life and (except where specifically adjusted) refer to the time lived after that date. There are two reasons for the selection of this arbitrary date: (1) Most of the reports used are those on birds banded as fledglings, not as nestlings—making an exact estimate of age impossible. (2) There is a strong possibility (suggested by the banding data themselves) that a bird which dies near the place where it was banded prior to its first migration is more likely to be recovered than one that dies after the beginning of the first migration; hence the use of recoveries made before the beginning of the first migration would give a disproportionate weight in the sample to those young birds which die before this time. Lack (1943*a*) selected August 1 as the date upon which to base his longevity and life-expectancy calculations. It appears that there is a strong possibility that the lower life expectancy (1.6 years) on the first August 1, as compared with that (1.9 years) on the second August 1, in *Turdus merula,* for instance, may be because the *rate of recovery* of first-year birds that die near the banding stations is greater than the rate of recovery of those dying elsewhere. It must be conceded, nevertheless, that this is a more difficult problem in the case of *Turdus merula* because a relatively small part of the population is migratory. Kraak *et al.* (1940) used January 1 as the basic date in their calculations for the Lapwing. In the studies described in this paper no differences in expectancy calculations were noted between those as of January 1 and those as of November 1. November 1 was therefore selected in order to reduce the period between the nest and the date of calculation as much as possible and yet allow for the banded young to be dispersed from the nesting localities.

It is unfortunate that, because of the reasons stated above, the data do not allow a direct calculation of the mortality during the critical period from the nest to the first November 1. However, a crude estimate (see below) of this mortality can be made by the use of data on the number of clutches, number of young produced per clutch, together with data on the replacement rate necessary to maintain a constant population. This estimate is obviously more accurate than one based on banding returns and recoveries.

Age-Group Composition

In calculating the general age-group composition of the Robin population, the total 855 recoveries and returns mentioned above were used and were classified according to year of life in which the individual was recovered. ("First year" birds are those recovered between the first and second November firsts of the bird's life; "second year" birds are those recovered between the second and third November firsts of the bird's life, etc.) It is assumed, as stated previously, that these recoveries and returns constitute a normal sample of the population. The records are classified into three regions according to banding localities (to which in almost all cases the banded young return as breeding adults). For the purposes of this study, three areas are used: (1) *Central* (Iowa, Illinois, Indiana, and Ohio), (2) *Northwestern* (Alberta, Saskatchewan, Manitoba, North and South Dakota, Minnesota, Wisconsin, and Michigan), and (3) *Northeastern* (Pennsylvania, New York, New Jersey, New England, and the Maritime Provinces). The data on age groups are summarized in Tables 1a and 1b.

TABLE 1a

General Age-Group Composition

Banding area	Total All ages	Year of life						Ratio Adult: Young	Survival rate[1]
		1st	2nd	3rd	4th	5th	6th+		
Central	293	150	80	46	9	6	2	95:100	49
Northwest	295	172	64	36	15	7	1	71:100	42
Northeast	245	116	67	34	21	4	3	111:100	53
Others[2]	22	16	4	1	0	1	0		
Total— All areas	855	454	215	117	45	18	6	88:100	48

[1] Per cent per annum after the first November 1, assuming a *stable* population. Survival rate = 100 — mortality rate. In a stable population the annual mortality rate equals the ratio of surviving first-year birds to the total population, since the number of young surviving from each year (taken in this study as those alive on their first November 1) is equal to the number of second-year and older birds which have died during the year, provided that the mortality rate is the same for each age group.

[2] Records from eastern Montana, eastern Wyoming, Ontario, and other localities within the range of *Turdus m. migratorius* but falling outside the three main geographical divisions of the range as defined in the text.

TABLE 1b

General Age-Group Composition
(Data from Table 1a expressed in percentage)

Banding area	Year of life						Ratio Adult:Young	Survival rate
	1st	2nd	3rd	4th	5th	6th+		
Central	51	27	16	3	2	1	95:100	49
Northwest	58	22	12	5	2	0	71:100	42
Northeast	48	27	14	8	1	1	111:100	53
All areas	53+	25+	14−	6−	2−	1−	88:100	48

It is obvious from the tables that the reduction in numbers from one age group to the next is fairly constant. That is, the apparent mortality rate is not differential according to age, at least in the first three age groups. Definite statements cannot be made about the older age groups because of the small number of records.

Nice (1937:194) has calculated the theoretical age-group composition for stable populations, basing the calculations on the annual survival rates and assuming that there is no difference in death rate among the various age groups. Since data presented subsequently in this paper, as well as the data in Table 1a, indicate that the mortality rate for Robins is approximately the same in all age groups, Nice's theoretical table is applicable to *Turdus migratorius*.[3] Table 2 gives the theoretical composition of populations with survival rates within the order of magnitude which may apply to this species. A comparison of Tables 1b

TABLE 2

THEORETICAL AGE-GROUP COMPOSITION ACCORDING TO ANNUAL SURVIVAL RATES [1]

Survival rate[2]	Per cent of total according to year-groups						Average longevity
	1st	2nd	3rd	4th	5th	6th+	
40	60	24	10	4	1	1	1.7 years
45	55	25	12	5	2	1	1.8 years
50	50	25	13	6	3	3	2.0 years
55	45	25	14	8	4	4	2.2 years

[1] Adapted from Nice (1937:194).

[2] Per cent per annum (after first November 1, as applied to Robin populations in this study).

and 2 shows that there is a reasonable similarity between the theoretical calculations and calculations from banding data.

The markedly lower survival of birds banded in the Northwest area is interesting and, if the sample is reliable, may be interpreted as indicating a higher reproductive rate in this area,[4] since recoveries of banded birds indicate no influx of Robins reared in other areas. However, if trapping data (data from birds recovered alive) are not used, the difference between Northwest and Northeast is not so marked, suggesting that a higher rate of trapping of first-year birds in the Northwest area or a higher rate of trapping of older birds in the Northeast area may enter the picture. Subsequent data in this paper show that these discrepancies are probably not important.

[3] Nice states that her table (from which Table 2 is adapted) is applicable only to species which breed during the first year, but it appears to be applicable to any species in which the death rate is the same for all age groups. Actually a decision on this point is probably not necessary insofar as this study is concerned, since all the available evidence indicates that Robins breed during the first year.

[4] It would be interesting to compare the average clutch sizes and numbers of broods of the three areas, but data are lacking in the literature, emphasizing again the need of *quantitative* observations on the life history of many of our common species of birds.

Of further interest is the comparison of the population of the wintering area with that of the breeding area (Tables 3a and 3b). For the former, Robins banded as young in the range of *Turdus m. migratorius* and recovered (either alive or dead) during December, January, and February in the Carolinas, Georgia, Arkansas, and the Gulf States, are used as the sample (a total of 303 records). These can safely be regarded as winter residents at the time and place of recovery. Robins banded as young in the northern states and recovered at or near the same locality during a subsequent breeding season (March to September) were assumed to constitute a sample of the Robin population (excluding the young of the year) in the breeding area (447 records). Birds recovered during the migration seasons were omitted from these samples.

Exact data are lacking, but available observations indicate that, exclusive of young of the year, a very large part of the breeding-area population of Robins as well as of many other passerine species are breeding birds. The data from trapping alone are analyzed separately to allow comparison with the data from all returns (Tables 3a and 3b). Table 3b presents no striking differences with the theoretical figures given in Table 2. It emphasizes the fact that for at least three years,

TABLE 3a

AGE-GROUP COMPOSITION AMONG WINTER-AREA AND BREEDING-AREA ROBINS

Population	Total All ages	Year of life						Ratio Adult:Young	Survival rate[1]
		1st	2nd	3rd	4th	5th	6th+		
Winter-area	303	153	73	46	22	9	0	98:100	49
Breeding-area[2]	447	229	118	65	21	8	6	95:100	48
Breeding-area[3]	153	90	37	18	6	0	2	70:100	41

[1] Per cent per annum after the first November 1.
[2] All birds recovered in the breeding area, whether alive or dead.
[3] Birds recovered alive in the breeding area.

TABLE 3b

AGE-GROUP COMPOSITION AMONG WINTER-AREA AND BREEDING-AREA ROBINS
(Data from Table 3a expressed in percentage)

Population	Year of Life						Ratio Adult:Young	Survival rate[1]
	1st	2nd	3rd	4th	5th	6th+		
Winter-area	51	24	15	7	3	0	98:100	49
Breeding-area[2]	50	26	14	5	2	2	95:100	48
Breeding-area[3]	59	24	12	4	0	1	70:100	41

[1] Per cent per annum after the first November 1.
[2] All birds recovered in the breeding area, whether alive or dead.
[3] Birds recovered alive in the breeding area.

after the first November 1, there is no differential mortality rate in respect to age among Robins.

Of particular interest is the comparison of the age-group composition of the wintering-area and breeding-area populations. The close similarity of these data indicate that migration mortality, at least during the northward migration, is the same in all age-groups. The larger percentage of first-year birds in the trapped sample is difficult to interpret; its significance may be questioned because of the small size of the sample, but a possible explanation is that the first-year birds are more easily trapped, as has been previously suggested in reference to the apparently lower survival of birds in the Northwest area. Data are lacking, however, to support this suggestion. An explanation based on a differential mortality rate must be rejected because it is not supported by data on birds recovered dead (Table 9).

General Mortality and Survival Rates

The mortality and survival rates for adult Robins (all birds past their second November 1), already calculated in Table 1a from the ratio of first-year birds in the sample to the total sample, may also be compared with these rates as obtained from an analysis of records of Robins banded as young and recovered dead subsequent to their first November 1 (Table 4).

TABLE 4

Age-Group Composition of Robins Recovered Dead

Banding area	Total All ages	Year of life						
		1st	2nd	3rd	4th	5th	6th	7th+
Central	201	103	52	32	6	6	1	1
Northwest	207	110	50	26	12	7	0	2
Northeast	160	73	50	16	18	2	1	0
All areas	568	286	152	74	36	15	2	3

TABLE 5

Survival in Robins

(Data derived from Table 4)

Banding area	Number alive on Nov. 1 of each year								Survival rate[1]
	1st	2nd	3rd	4th	5th	6th	7th+	Total	
Central	201	98	46	14	8	2	1	370	46
Northwest	207	97	47	21	9	2	3	386	46
Northeast	160	87	37	21	3	1	0	309	48
All areas	568	282	130	56	20	5	4	1065	47

[1] Per cent per annum.

In deriving the adult mortality rate from the data in Table 4, cumulative totals of all birds alive on the various November firsts were computed (Table 5). The computations take into consideration the fact that the number of birds alive on the fourth November 1, for example, are those which were recovered in the fourth, fifth, sixth, and seventh years; those alive on the fifth November first are those which were recovered during the fifth, sixth, and seventh years, etc. The total number of birds alive on the various November firsts represents the composite strength of the sample. Adult mortality rate is then obtained by dividing the total number of deaths (first column, Table 4) by the composite strength of the sample (total number alive on all November firsts).

The survival rates in Table 5 are more accurate than those in Tables 1a and 1b since the calculations in the former take into account the age differences in mortality whereas those in Tables 1a and 1b assume it to be constant. This may account for the greater geographic uniformity in the rates in Table 5, although there is the possibility that the greater divergence in the rates in Table 1a may be due in part to age selectivity in trapping since no trapping recoveries or returns are used in the calculation of the rates in Table 5.

It is important to emphasize that these calculations are based on a small sample scattered over 20 years and over a broad geographical area. Whereas the figures may approximate true means for the entire

TABLE 6

Comparison of Survival Rates for Various Passerine Species

Species	Survival rate[1]	Source
Turdus migratorius American Robin	47	This paper, Table 5
Turdus merula merula European Blackbird	52[2]	Lack (1943*a*)
Turdus ericetorum ericetorum Song Thrush	47[3]	Lack (1943*b*)
Melospiza melodia euphonia Song Sparrow	45–60[4]	Nice (1937)
Erithacus rubecula melophilus English Robin	33[3]	Lack (1943*d*)
Sturnus vulgaris Starling	50	Kluijver (1933, 1935)
Sturnus vulgaris Starling	50[3]	Lack (1943*b*)

[1] Per cent per annum.

[2] Lack's statement that "about 40 per cent of the adults die each year" appears to cover birds after they had reached their second August 1. His survival data are here recalculated to include all birds after they had reached their first August 1. The method of calculation is that used in Table 5.

[3] Lack's data recalculated according to the method used in Table 5.

[4] The higher survival rate represents a period of optimum conditions; the lower, a period in which the cover was largely removed.

area, it must be remembered that all natural populations fluctuate both geographically and temporally. These fluctuations are accompanied by changes in the age-group composition, in survival and mortality rates, and in mean longevity. Detailed knowledge of these fluctuations in Robins must await the accumulation of much larger numbers of recoveries of Robins banded as nestlings or fledglings as well as extensive investigations at individual banding stations throughout the breeding range of *Turdus migratorius.* An idea of the nature of temporal fluctuations in a passerine species can be obtained from the studies of Nice (1937). It is of interest to compare the survival rates (per cent per annum) of the various passerine species for which they have been recorded (Table 6).

It is interesting to compare the rates compiled in Table 6 with those obtained in studies on non-passerine species. Because of differences in sampling methods and other variables, such comparisons must be made with caution, but it is probable that the figures indicate general similarities or differences in survival rates. Among the galliform species Sumner (1935), Richardson (1941), and Emlen (1940) have found survival rates of 27, 28, and 33-48 per cent respectively for California Quail in California. Leopold *et al.* (1943) gave a survival rate of 30 per cent among Ring-necked Pheasants in the University of Wisconsin Arboretum.

Likewise several studies give rates for charadriiform species. Kraak *et al.* (1940) calculated a survival rate of 60 per cent for the Lapwing. Lack's data (1943*c*) for the same species (recalculated by the method in Table 5) indicate a rate of 64 per cent. In these studies all types of recoveries and returns were used. Laven's (1940) studies with banded Ringed Plover (*Charadrius hiaticula*) indicate a survival rate of about 50 per cent. A recalculation of the data of Lack (1943*c*) for the European Woodcock (*Scolopax rusticola*) gives a survival rate of 54 per cent. Lack's sample consisted largely of birds recovered by shooting; he assumed that the older birds were shot as easily as the young but admits that this assumption is unproved.

Lack (1943*c*) also gives a survival rate of 67 per cent (58 per cent when recalculated) for the Black-headed Gull (*Larus ridibundus ridibundus*). Lewis (1930) calculated that the annual survival rate in a breeding population of Atlantic Murres (*Uria aalge aalge*) was about 95 per cent.

Williams (1944:253) has made an interesting study of the Redhead (*Nyroca americana*) based on birds banded as young and shot by hunters. The data show that 87 per cent of the birds taken were less than one year old. These data, if the birds were considered to constitute a normal sample of the population, would indicate a survival rate of only 13 per cent. Lack (1943*c*) has shown that samples obtained by shooting in some of the larger non-passerine species are not normal samples but contain disproportionately large numbers of first-year birds. Because of the number of variables involved, no generalizations can be made concerning the selectivity of shooting as a sampling method. Actually, each species will require separate investigation on this point. Data from Hochbaum's (1944:133) careful investigation likewise would indicate a low survival rate (8 per cent per annum) if a shooting sample (92 per cent juveniles) is accepted as normal for the population. Hochbaum's data on other species of ducks give somewhat lower percentages of young in shooting bags—from 56 per cent juveniles in the Pintail (*Anas acuta tzitzihoa*) to 87 per cent juveniles in the Canvas-back (*Nyroca valisineria*). Until trapping or other types of data verify these ratios it is, as indicated above, unsafe to use them in calculations of longevity or as an index to survival rates and age-group composition of duck populations.

Longevity

For the purposes of this study, several terms involving longevity are used. *Potential longevity* is the maximum life span that can be attained by an individual of the species. The best indications of potential longevity are obtained from the records of longevity under optimal or near-optimal conditions such as in zoos. *Natural potential longevity* is the maximum life span that can be attained in nature. The best estimates of this can be obtained from the greatest ages attained by banded wild birds. The *turnover period* (Leopold *et al.*, 1943) is the time required for a year class (i.e. the birds hatched during a single season) to shrink to statistical zero, or the reduction of any single year class to the point where it no longer constitutes a significant portion of the population. Individual birds may outlive the turnover period but do not represent a significant portion of the population. In the case of the American Robin a general idea of the turnover period can be obtained from Table 1b, which indicates that this period is about six years. Separate compilations for year classes tend to verify this figure, although a more precise determination must await a larger accumulation of data on birds banded as young.[5] *Average natural longevity* is the mean age attained by members of the species in nature. In this paper it is based on birds that have survived the first November 1. Average natural longevity for a population of birds can be obtained in one of two ways: (1) By calculating the mean age of birds recovered dead, regarding them as a normal sample of the population. (2) By calculation from the ratio of young birds to adults which, in a stable population, indicates the annual adult mortality rate. Burkitt (1926:97), in his studies on the English Robin (*Erithacus rubecula melophilus*), pointed out that if the population remains constant and if the annual mortality rate (M) is known, the average natural longevity (Y) can be calculated, that is, $Y = \frac{1}{M}$. Burkitt corrected the formula as applied to *Erithacus rubecula* to allow for the non-breeding portion of the

[5] Leopold *et al.* (1943:390) found the turnover period in a local Pheasant population to be five years.

population, but since similar data are not available for *Turdus migratorius*, a discussion of the complete formula is not included here. Burkitt calculated the average natural longevity of *Erithacus rubecula* to be 2.8 years. However, Lack (1943*d*:130) has indicated that an erroneous assumption was probably made in estimating the number of young in relation to the number of adults and that the average natural longevity is about 1.1 years for those birds that survive to their first August 1.

Because the age calculations in this study are based on the first November 1 of the life of the bird, and because most of the birds had been banded as fledglings rather than as nestlings so that their precise ages are not known, it has been necessary to estimate an average age for the young on their first November 1. A careful consideration of the data compiled by Howell (1942:546) on nesting dates leads to an estimate of five months (0.4 years) as the average age of young Robins on their first November 1.[6] This figure has been added to the average

TABLE 7
AVERAGE NATURAL LONGEVITY (*Y*) IN ROBINS
(Based on birds surviving to their first November 1)

Area	Calculation A[1]		Calculation B[2]		Mean age of birds recovered dead		
	Mortality rate[3]	*Y*	Mortality rate	*Y*	No.	*Y* 1st Nov. 1[4]	Total *Y*[5]
Central	54	1.85 yrs.	51	1.9 yrs.	207	1.3 yrs.	1.7
Northwest	54	1.85 yrs.	58	1.7 yrs.	201	1.3 yrs.	1.7
Northeast	52	1.9 yrs.	47	2.1 yrs.	160	1.4 yrs.	1.8
All areas	53	1.9 yrs.	52	1.9 yrs.	568	1.3 yrs.	1.7

[1] Using survival rate from Table 5.
[2] Using survival rate from Table 1a.
[3] Per cent per annum.
[4] Calculated by averaging time in months elapsed from first November 1 to date when recovered for all birds in sample and converting to years.
[5] By addition of 0.4 years, the estimated mean age of Robins on their first November 1 (see text).

longevity as calculated from the first November 1. Table 7 gives the figures for average natural longevity calculated from the mortality rates and by averaging the ages at death of birds banded as young.

There is an average discrepancy of 0.2 years between the average longevity (*Y*) as calculated from the mortality rate and as com-

[6] Howell's data, based on 147 nesting records at Ithaca, New York, indicate that the nesting season (as determined by the laying of the first egg) extends from about April 10 to July 24, with May 21 as the average date for the laying of the first egg of the clutch. Allowing 16 days for the completion of the clutch and for hatching would give the average hatching date as June 6, and an average age on November 1 of about five months. Howell's compilation from the literature for other states in the breeding range of *Turdus m. migratorius* gives similar figures.

puted from the recoveries of dead birds of known age. There are at least two possible explanations: (1) the average age of young birds on the first November 1 may be greater than the estimated 0.4 years; (2) more deaths may occur in the first part of the November 1-October 31 year than during the latter part. The second explanation is possible because part of the fall migration and all of the spring migration occur between November 1 and May 1. Furthermore, severe weather conditions are more frequent during that part of the year. The data tend to support the second explanation, though these may indicate merely that more birds are recovered during the first part of the year rather than that more birds die then.

Average natural longevity data are available for a few other species. These are compiled in Table 8. Because of the variety of methods used

TABLE 8

Average Natural Longevity (Y) of Some Species of Birds

Species	No. of records	Y in years	How obtained	Reference
Turdus migratorius American Robin	855	1.7	R	This paper
Turdus migratorius American Robin	568	1.9	C	This paper
Turdus merula merula European Blackbird	352	1.8	C	Lack (1943*a*)
Turdus ericetorum ericetorum Song Thrush	374	1.7	C	Lack (1943*b*)
Erithacus rubecula melophilus English Robin	130	1.3	C[1]	Lack (1943*d*)
Melospiza melodia euphonia Song Sparrow	64	2.7	R[2]	Nice (1937)
Melospiza melodia euphonia Song Sparrow	144	1.5	R[3]	Nice (1937)
Carpodacus purpureus Purple Finch	621	2.0	E	Magee (1928)
Sturnus vulgaris Starling	205	3.0	C[4]	Kluijver (1935)
Sturnus vulgaris Starling	203	2.0	C	Lack (1943*b*)
Vanellus vanellus Lapwing	1333	2.5	C[5]	Kraak *et al.* (1940)
Vanellus vanellus Lapwing	460	2.8	C[5]	Lack (1943*c*)
Scolopax rusticola European Woodcock	203	2.2	C[5]	Lack (1943*c*)

R = longevity (Y) obtained by averaging the ages at death of birds banded as young and subsequently recovered dead.

C = longevity (Y) obtained by calculation from mortality rates as given in Table 6. Mortality rate (M) = 100 — survival rate. $Y = \frac{1}{M}$

E = estimated longevity (Y) based on returns of birds banded as adults.

[1] Verified by observation.

[2] "Normal conditions."

[3] "Unfavorable conditions." Cover removed. Nice states that the figure may be too low.

[4] This is for breeding birds only and is too high for the general population.

[5] Includes relatively large numbers collected by shooting.

in these studies, comparisons should be made with considerable care. In general, these data give average natural longevity for birds that have survived the critical fledgling period and have reached an age when the mortality rate is about the same as that of the adult birds. Thus the estimates for *Turdus migratorius* are based on those birds that have survived the November 1 following hatching; Lack's calculations are based on the birds alive on the August 1 following hatching; those of Kraak *et al.* on the birds of the January 1 following hatching; and those of Nice on the birds alive at the beginning of the first breeding season. Also, it should be noted that the longer the time between hatching and the date of calculation, the greater the figure for the average natural longevity becomes because of the elimination of the records of those birds that die early. If *all birds hatched* were included, the figure for the average natural longevity in all cases would, of course, be much lower.

Average Natural Longevity Compared with Potential Longevity

An idea of the potential natural longevity can be obtained from the greatest ages attained by banded birds. Among the records used in this study are one of a Robin recovered dead in its ninth year and one in its sixth year. Cook (1942:114, 1943:73) lists one record of at least eight years, two of at least seven years, and three of at least six. Her previous list (1937:61) contains records of one Robin at least seven years old, and one which was at least six years old at the time of recovery. Similar data are available for other species of the genus *Turdus*. For *Turdus ericetorum,* Lack (1943*b*:196) gives one eight-year record as well as records of one seven-year and two six-year birds. He also (1943*a*:168) gives two records of at least nine years for *Turdus merula,* two of at least eight years, and five of at least seven. On the other hand, reports from the continent do not give ages which approach these. For example, the oldest *Turdus merula* reported by Drost (1930:82) is "at least" four and one-half years; Schenk (1924:153) gives none over "at least" two years.

Very few data are available on the potential longevity of *Turdus migratorius*. Mitchell (1911:470) gives the maximum age attained by this species in captivity. Eleven individuals had an average "zoo-longevity" of 5.1 years. The greatest age attained was 12.9 years, which was also the greatest attained by any of the 68 Turdidae recorded by him. In none of these cases was the age of the bird at the beginning of captivity known. Records are available for other members of the genus *Turdus*. Gurney (1899:35) gave two records for *Turdus merula* of at least 20 years; he also lists records of 15 and 17 years for *Turdus musicus* [= *ericetorum*]. Flower (1926:1371) states that *Turdus ericetorum philomelus* can survive 15 to 17 years in captivity and *Turdus merula* up to 20 years.

In view of these data it seems safe to assume that the potential natural longevity of *Turdus migratorius* is at least 9 or 10 years. The potential longevity is at least 12 years, and, considering records of other members of the genus, it may be as much as 20 years. Obviously, the average Robin lives through only a fraction of its potential life span. This fact may, to some degree, eliminate both experience and physiological old age or senescence as factors in age-group composition of populations and may explain the apparently non-differential death rate. In other words, it is possible, if mortality rates in Robins are affected by experience over a period of years or by physiological old age, that the vast majority die before they reach the age at which these factors become effective.

Life Expectancy

Life expectancy (*e*) as used in this paper is the mean time elapsed between the selected date(successive November firsts in Table 9) and the time of death (actual date recovered dead) for all birds alive on the selected date. In other words, it is the expectancy of further life for the average Robin on the selected date. Expectancy data are tabulated according to geographical areas and according to samples in which death was due to shooting and predation by cats (Table 9). In general, the expectancy calculations beyond the third November 1 cannot be regarded as reliable because of the small number of records available. The expectancy for the fourth November 1, based on 56 records, was one year.

Table 9 demonstrates that, for first-, second-, and third-year Robins, life expectancy is about the same (1.1 to 1.4 years). Also, mortality rates are similar for all age groups in the samples in which death was

TABLE 9

Life Expectancy (*e*) on Successive November Firsts

Description of sample			*e* in years[1]		
Area	Cause of death	Number dead	1st Nov. 1	2nd Nov. 1	3rd Nov. 1
Central	All causes	201	1.3	1.1	1.1
Northwest	All causes	207	1.3	1.3	1.1
Northeast	All causes	160	1.4	1.2	1.3
All areas	All causes	568	1.3	1.2	1.2
All areas	Shot	61	1.3	1.2	—
All areas	Killed by cat	55	1.4	1.2	—

[1] For each Robin recovered dead the time elapsed between the selected November 1 and the date of death (actual date recovered), was calculated to the nearest month from its card in the United States Fish and Wildlife Service files. The expectancy for any particular November 1 was then obtained by calculating the mean period from the selected November 1 to date of death for all birds which were alive on that November 1. For convenience in comparison with other authors the means were then expressed to the nearest tenth of a year.

due to shooting and predation by cats, suggesting uniform mortality rates regardless of the cause of death. This is an important point since, if there are no age-differentials, it is not necessary to attempt to weight the components of the sample. Death in Robins, as well as in other passerine species, is apparently a matter of chance and largely independent of age once the birds have survived the critical fledgling period. Taking the sample as a whole, it can be said that after the first November 1 slightly more than 50 per cent die each year.

In this country Thomas (1934:126) has shown that very few Starlings reach the age of five years; a "fair number" live four years; and considerable numbers live three. Hoffman (1929:56) states that 28 per cent of the young of the Blue Jay survive to breed once and 9 per cent to breed twice. The calculations were based on the assumption that all birds banded as young and still alive were retrapped, and therefore the resulting figures are probably too low. Nice's excellent study (1937) does not give sufficient data on exact ages at death to permit a calculation of life expectancy. The data of Harold and J. R. Michener (1933) on the House Finch indicate a life expectancy which may be somewhat higher than that of *Turdus migratorius*. For comparison the expectancy figures for *Turdus migratorius* are given in Table 10 with Lack's figures for other species. (The data given by Austin, by Williams, and by Hochbaum are not usable for comparison here for the reasons given above.)

TABLE 10

Comparative Life Expectancy (*e*) Chart for Several Species of Birds

Species	First day of year	No. alive 1st day of year	*e* in years on 1st day of successive years					Reference
			1st	2nd	3rd	4th	5th	
Turdus migratorius American Robin	Nov. 1	568	1.3	1.2	1.2	1.0	—	This paper
Turdus merula merula European Blackbird	Aug. 1	352	1.6	1.9	1.7	1.9	1.8	Lack (1943*a*)
Sturnus vulgaris Starling	Aug. 1	203	1.5	1.4	1.4	—	—	Lack (1943*b*)
Turdus ericetorum ericetorum Song Thrush	Aug. 1	374	1.4	1.6	1.4	1.3	—	Lack (1943*b*)
Erithacus rubecula melophilus English Robin	Aug. 1	130	1.1	1.3	—	—	—	Lack (1943*d*)
Vanellus vanellus Lapwing	Aug. 1	175	2.4	2.5	2.5	2.5	2.2	Lack (1943*c*)
Larus ridibundus ridibundus[1] Black-headed Gull	Aug. 1	130	1.8	2.4	2.4	2.2	2.9	Lack (1943*c*)

[1] Records of shooting recoveries not included.

Calculation of Mortality Among Young Prior to November 1

There are no data available that can be used to fix accurately the mortality rate among young Robins from the time of fledging until the following November 1. The calculations in this section are indirect and to a certain extent hypothetical. They are intended only to indicate broadly the mortality for this period. It is hoped that actual observations will eventually verify or modify these calculations.

The ratio of young to adults in the Robin population as determined from the data in Table 1a is 100 young to 88 adults. This means that in a stable population the breeding survivors of each 100 adults alive on November 1 must produce a number of young alive on the following November 1 sufficient to maintain this ratio. A conservative estimate of the adult mortality between November 1 and the breeding season is 25 per cent, since the mortality rate is slightly more than 50 per cent for the entire year. Hence 75 of each 100 Robins alive on November 1 survive to breed during the following breeding season. Furthermore, of each 100 Robins alive on November 1, only 47 are alive on the following November 1. Therefore the estimated 75 (37 pairs) alive during the breeding season must produce 53 (1.4 per pair) young alive on the following November 1 in order to maintain the ratio. The calculations may be summarized as follows:

November 1	47 adults, 53 young
May 1	75 breeding birds (37 pairs)
November 1	47 adults, 53 young (1.4 young per breeding pair)

Mason (1943:75) found the average number of nestlings in 86 nests at Groton, Massachusetts, to be 2.86 per nest. Assuming that each pair rears two broods per year, each pair would produce, theoretically, 5.7 young per season. Howell (1942:594) estimates that each pair rears 3.9 young per season (based on data from 74 nests). It is not clear whether he refers to nestlings or fledglings. Should the reference be to fledglings, his results are close to those of Mason, since it is reasonable that 5.7 nestlings would result in 3.9 fledglings. Another estimate can be obtained by combining the observations of Mason and Howell: three nesting attempts times 54 per cent success (Howell, 1942:594) times 2.86 nestlings per successful nest (Mason, 1943:75) gives 4.6 nestlings per pair per season.[7] Thus it seems reasonable to assume that from somewhat less than four to slightly more than five young may be fledged per average pair per season. The mortality from the time of fledging to the first November 1 would then be about 70 per cent.

Since the annual mortality rate after the first November 1 is 52 per cent, about 25 per cent of the young alive on November 1 must die before May 1, so that only about 20 per cent of the fledged young

[7] Nice (personal communication) found an average of 4.4 young per nest for *Turdus migratorius achrusterus* in Oklahoma.

actually survive to breed. Nice (1937:186) estimated that 15 to 25 per cent of the fledged Song Sparrows survived to breed. Similar results were recorded by Kendeigh (1934) and Kluijver (1935) for the House Wren (*Troglodytes aëdon*) and the Starling respectively, although in the latter case the calculations are complicated by the fact that not all Starlings breed during their first year.

Summary

Data from 855 Robins (*Turdus migratorius migratorius*) banded as young and subsequently recovered were studied from the standpoint of age groups, longevity, and life expectancy.

The age-group composition of the Robin population throughout the range of the northern race (excluding young that have not reached their first November 1) was found to be as follows: 1st year birds, 53 per cent; 2nd year, 25 per cent; 3rd year, less than 14 per cent; 4th year, less than 6 per cent; 5th year, less than 2 per cent; and 6th year or older, less than one per cent.

The ratio of adults to young of birds throughout the range was found to be 88:100. In the northeast area, it was found to be 111:100.

The mortality rate for all birds that have passed their first November 1 is slightly more than 50 per cent per annum. The mortality rate is probably the same for all age groups.

The age-group composition in the wintering-area population is similar to that in the breeding-area population, indicating that there is no differential mortality rate according to age during spring migration.

The adult survival rate of *Turdus migratorius* (47 per cent per annum), as determined in this study, is slightly lower than that of other members of the genus for which it has been determined.

The average natural longevity of Robins that survive their first November 1 is about 1.7 years. This is comparable with the figures for other passerine species.

The average natural longevity (1.7 years) is only a fraction of the potential natural longevity (at least 9 years) and of the potential longevity (at least 13 years, perhaps as much as 20 years).

The turnover period is about six years.

Life expectancy from the first November 1 to the third November 1, and hence for more than 90 per cent of the population, is 1.2 to 1.3 years and apparently does not change with the age of the bird. These results are in agreement with those for European passerine species.

Life-expectancy figures calculated from the number of birds shot and from the number of birds killed by cats were similar to those calculated from the total sample.

A hypothetical calculation indicates that the mortality rate from the nest to November 1 (an average of about 5 months) is probably 70 per cent, as compared with an estimated adult mortality rate of about 25 per cent for the same five-month period.

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